Heterotheca Benson; Lyginopterid pollen organs or coprolites?

G. W. Rothwell[1] and A. C. Scott[2]

[1]Department of Botany, Ohio University, Athens, Ohio 47501, U.S.A.
[2]Geology Department, Royal Holloway and Bedford New College, Egham, Surrey TW20 0EX

Synopsis

A reinvestigation of the originally described specimens of *Heterotheca grievii* Benson, putative pollen organ of the Lower Carboniferous plant *Heterangium grievii*, reveals that all are coprolites.

Introduction

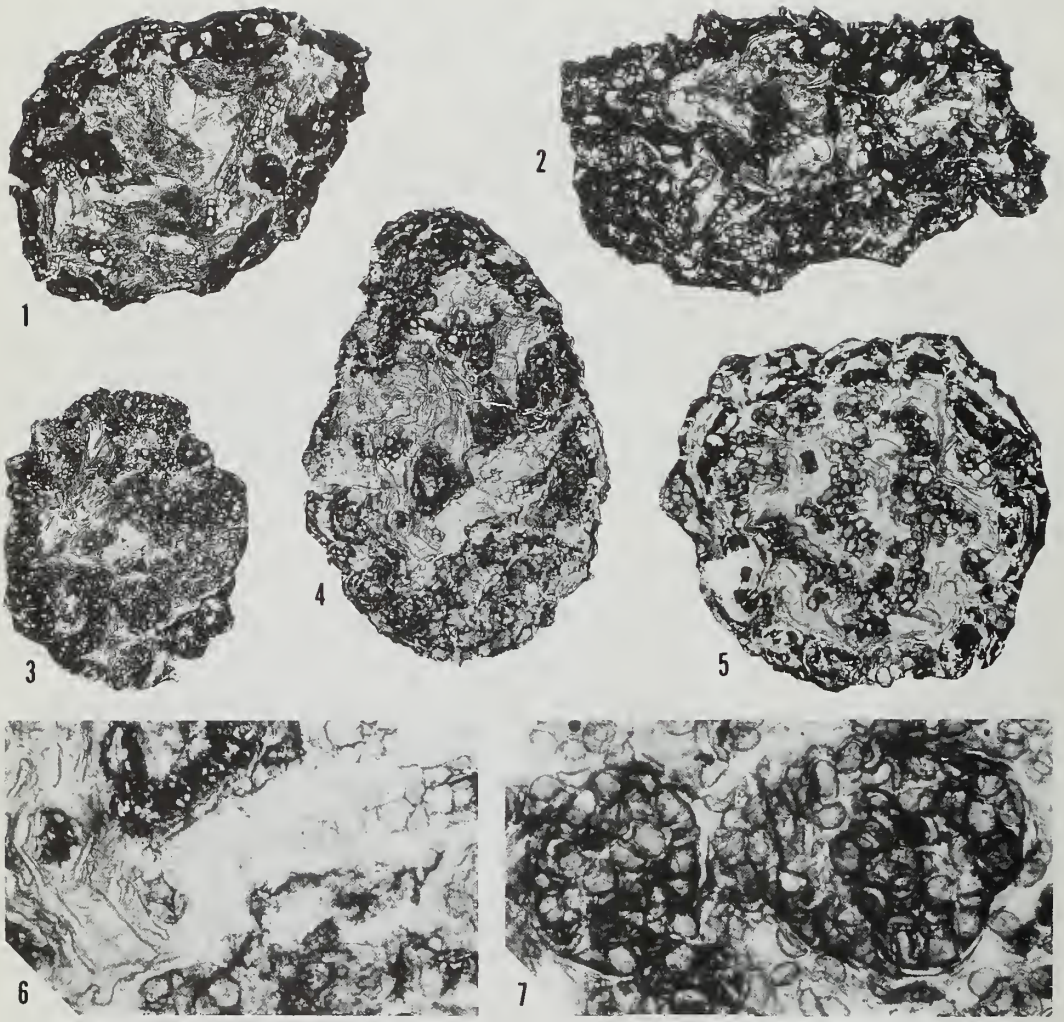
The description of *Heterotheca grievii* Benson (1922) established a record of putative lyginopterid pollen organs in Lower Carboniferous strata, and provided a structural model for interpreting evolution among microsporangiate fructifications of the most primitive gymnosperms (Benson 1922, Schopf 1949). Specimens occur within blocks of permineralized peat collected on the beach near Pettycur, Fifeshire, Scotland (Gordon 1909), and are late Viséan in age (Gordon 1909, Scott *et al.* 1984). Additional specimens of *Heterotheca* have not been reported, but a reconstruction has been offered (Schopf 1949). The generic name has also been changed to *Bensoniotheca* because *Heterotheca* was used earlier for a genus of extant angiosperms (Mickle & Rothwell 1979).

Description and Discussion

Benson described *Heterotheca* from 60 specimens. Twenty-three of these are now housed in the Department of Palaeontology, British Museum (Natural History), and together with new material from Pettycur, are the data upon which this investigation is based. The specimens are irregularly subspheroidal–ellipsoidal, ovoid in cross sections, 1 mm in diameter, and 3·5–4·0 mm long (Figs 1–5). They have an undulating outer surface, and no consistent internal structure or histological features (Figs 1–5). Most specimens consist of heterogeneous fragments of plant tissue (e.g. Fig. 6), but a small number are represented by masses of spores (Figs 3, 7). The spores occur as irregularly-shaped aggregates of variable density, but they are not surrounded by a cellular envelope and do not represent sporangia. At the periphery of many specimens the material is darker than in the center (Figs 1, 2).

Heterotheca conforms to the structure of coprolites that are commonly encountered in Carboniferous and more recent strata (Scott 1977, Baxendale 1979, Rothwell & Scott 1983, Scott & Taylor 1983). From the content of the specimens, it is clear that they were produced by herbivores (phytophagous arthropods), several groups of which were present in the Lower Carboniferous. Of these, *Heterotheca* specimens are most similar to the size range of faecal pellets produced by millipedes (Scott & Taylor 1983). The relatively consistent size and heterogeneous content of the specimens suggests that they represent the faeces of a single type of animal with a relatively nonspecific diet. However, a small number of specimens consist almost entirely of spore exines, and this introduces the possibility that two or more animals of similar size but differing diet may have produced the coprolites.

Heterotheca is the second type of putative seed-fern pollen organ to have been recently recognized as coprolites. The first, *Thuringia callipteroides* Remy, had been attributed originally to Permian callipterid foliage (Meyen 1984). *Heterotheca* and *Thuringia* have both contributed significantly to a misunderstanding about the structure of early seed-fern microsporangia and to the misinterpretation of gymnospermous evolution. This emphasizes the difficulties inherent in characterizing taxa from poorly-preserved specimens where sporangia cannot be separated clearly from faecal pellets containing pollen and spores.



Figs 1–7 Sections of *Heterotheca grievii* coprolites. All specimens housed in the Department of Palaeontology, British Museum (Natural History). Figs 1–2, specimens composed of cellular debris showing irregular shapes, surface features and internal structures: note darker colour of material near periphery of specimens. Fig. 1, slide 387-10 (Specimen C), × 32. Fig. 2, slide 395-6 (Specimen B), × 32. Fig. 3, specimen composed almost entirely of spores; slide 307-18, × 32. Figs 4–5, specimens similar to those in Figs 1–2 except that the peripheral area is not distinctly darker. Fig. 4, slide 387-10, × 50. Fig. 5, slide 386-12, × 50. Fig. 6, enlargement of cellular debris from specimen in Fig. 4; slide 387-10, × 80. Fig. 7, enlargement of sporogenous contents from specimen in Fig. 3; slide 307-18, × 160.

One additional point about our understanding of these fossils concerns nomenclature. The name *Heterotheca* Benson is illegitimate for plant remains because it is a later homonym of *Heterotheca* Cassini (Mickle & Rothwell 1979). However, the recognition that specimens of *Heterotheca* Benson represent coprolites removes the name from consideration under the Botanical Code (Voss *et al.* 1983). The name, however, is also preoccupied in zoology (Stechow 1921: 260), so if it is felt desirable to give these coprolites any 'generic' name as zoological ichnofossils, the replacement name *Bensoniotheca* Mickle & Rothwell (1979) is available for this purpose.

Acknowledgements

We thank Cedric Shute, Department of Palaeontology, British Museum (Natural History), for his assistance in locating the specimens of *Heterotheca*, and for the use of photographic equipment. This study was supported in part by a grant from the National Science Foundation (BSR83-10576 to G.W.R.) and a grant from the Natural Environmental Research Council (GR3/4986 to A.C.S.).

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